Communications

Ecological Applications, 19(8), 2009, pp. 1967–1974

Exploited reefs protected from fishing transform over decades into conservation features otherwise absent from seascapes

Graham J. Edgar,[1] Neville S. Barrett, and Rick D. Stuart-Smith

Tasmanian Aquaculture and Fisheries Institute, University of Tasmania, Private Bag 49, Hobart, Tasmania 7001 Australia

Abstract. Tasmanian reef communities within "no-take" marine protected areas (MPAs) exhibited direct and indirect ecological changes that increasingly manifested over 16 years, eventually transforming into communities not otherwise present in the regional seascape. Data from 14 temperate and subtropical Australian MPAs further demonstrated that ecological changes continue to develop in MPAs over at least two decades, probably much longer. The continent-scale study additionally showed recently established MPAs to be consistently located at sites with low resource value relative to adjacent fished reference areas. This outcome was presumably generated by sociopolitical pressures and planning processes that aim to systematically avoid locations with valuable resources, potentially compromising biodiversity conservation goals. Locations that were formerly highly fished are needed within MPA networks if the networks are to achieve conservation aims associated with (1) safeguarding all regional habitat types, (2) protecting threatened habitats and species, and (3) providing appropriate reference benchmarks for assessing impacts of fishing. Because of long time lags, the ubiquity of fishing impacts, and the relatively recent establishment of MPAs, the full impact of fishing on coastal reefs has yet to be empirically assessed.

Key words: *Australia; effects of fishing; long-term monitoring; marine protected area; reef fishes; sea urchins; temperate and subtropical reefs; threatened species; trophic cascades.*

Introduction

With the approach of 2012, the target year agreed under the Convention on Biological Diversity to "effectively establish, in the marine area, a global network of comprehensive, representative and effectively managed national and regional protected area systems" (United Nations Environment Programme 2005), governments worldwide are increasingly expanding networks of marine protected areas (MPAs). Although MPAs can be declared for fisheries enhancement, tourism, education, or a variety of other purposes, biodiversity conservation is most frequently cited as the primary goal of MPA networks (Leslie 2005). During planning for this goal, MPA declaration nevertheless also inevitably involves compromises aimed at minimizing impacts on existing resource users.

Stakeholder considerations are traditionally taken into account through subjective inputs to planning. More recently, quantitative MPA-selection algorithms that maximize representation of habitat types within MPAs while minimizing impacts on existing resource users have been recommended (e.g., Richardson et al. 2006, Klein et al. 2008, Smith et al. 2009).

Sociopolitical concessions can, however, lead to systematic biases in representation of particular biodiversity features within the MPA network (Lynch 2006, Edgar et al. 2008), both in terms of mappable habitat targets (Williams et al. 2009) and also community-types distributed within habitats (Harborne et al. 2008). For one important habitat type—shallow rocky reefs—we here assess the extent to which selection biases compromise the role of MPAs in achieving biodiversity goals. We use decadal temporal scale and Australia-wide spatial scale data sets to quantify (1) the magnitude of ecosystem change associated with protection of fished habitats within MPA networks, (2) the extent to which communities at highly fished locations transform following long-term protection into communities not otherwise present in the seascape, and (3) the degree to which MPAs are located at sites with low resource value.

As with other MPA monitoring programs, outcomes described here represent more than correlative observations; they describe results of a vast exclusion experi-

Manuscript received 10 April 2009; accepted 11 May 2009. Corresponding Editor: P. K. Dayton.
[1] E-mail: g.edgar@utas.edu.au

ment into effects of fishing conducted at a geographic scale meaningful for addressing management questions (Walters and Holling 1990). Geographic scale limitations were overcome in part through the assistance of skilled volunteer divers trained in underwater visual census methods through the Reef Life Survey program (program information *available online*),[2] allowing a continental-scale field assessment of ecological changes associated with MPA protection.

Methods

Analysis of Tasmanian long-term trends

Changes in subtidal reef assemblages within MPAs and at nearby fished reference sites were assessed off eastern Tasmania over a 16-year period. Surveys were undertaken within a 200-km long section of coast that includes Tasmania's longest-established "no-take" MPAs—the Maria Island National Park marine extension and two smaller southeastern Tasmanian marine reserves at Ninepin Point and Tinderbox (Barrett et al. 2009).

Quantitative underwater visual surveys of fishes, macroinvertebtrates, and macro-algae were undertaken in autumn each year, and spring in some years, from 1992 (six months after declaration of MPAs) to 2008, with the exception of 2003. For each survey, a total of six sites in the "no-take" sanctuary zone (SZ) and six sites in adjacent fished zones (FZ) at Maria Island were surveyed, and three SZ sites and four FZ sites in the southeastern Tasmanian marine reserves at Tinderbox and Ninepin Point. Data from the two small reserves were grouped because of their close proximity and low level of site replication within each.

Field survey protocols are described by Edgar et al. (1997). Divers laid four 50-m transect lines along the 5-m isobath at each site. The number and size of all fishes sighted within 5 m of the line were recorded for each side of the transect line, as were rock lobsters and sea urchins within 1 m of one side of the line. Thus, a total area of 2000 m^2 was surveyed for fishes at each site and 200 m^2 for macroinvertebrates. Total length estimates for fishes were binned in 25-, 50-, 75-, 100-, 125-, 150-, 200-, 250-, 300-, 350-, 400-, and 500-mm size classes, while lengths of fishes larger than 500 mm were individually estimated. Carapace lengths of all rock lobsters captured (~50% of animals sighted) were measured using callipers.

Fish abundance counts and size estimates were converted to biomass estimates using length–mass relationships available for each species (in some cases genus and family) in Fishbase (*available online*).[3] Bias in divers' perception of fish size underwater was additionally corrected using relationships presented in Edgar et al. (2004*a*). Because estimates of fish abundance can be greatly affected by fish behavior (Edgar et al. 2004*a*), biomass determinations are used here in a relative sense, rather than considered to provide an accurate absolute fish biomass estimate. Rock lobster biomass (B; in g) was estimated from carapace length (L; in cm) using the relationship $B = 0.000271 \times L^{3.135}$ (Edgar and Barrett 1999).

Effects of MPA protection were assessed for fishery species using the two metrics of (1) biomass of fishes >45 cm and (2) biomass of rock lobsters per 50-m^2 transect block, while secondary trophic effects of protection were assessed using two grazing pressure metrics: (3) density of gastropods and (4) density of sea urchins per 50-m^2 transect block. For each survey and metric, the mean of site SZ values was divided by the mean value for adjacent FZs, and the calculated SZ/FZ ratio presented graphically as a running mean for five successive surveys.

Long-term ecological change in MPAs was related to spatial variability in assemblage types within the broader southeastern Tasmanian region using multidimensional scaling (MDS) based on data on mean estimated biomass of all fish species sighted along transects at 34 sheltered to submaximally exposed sites surveyed (Edgar et al. 1997). This data set comprised the 10 FZ sites and nine SZ sites investigated in the initial year (1992) and concluding year (2008) of the Tasmanian MPA monitoring program, plus an additional 15 regional reference sites (RZ) surveyed in fished zones within the broader region during investigations in 1992–1994 (Edgar et al. 1997). Biomass data were square root transformed to reduce the influence of species with extremely high biomass. Paired site similarity was calculated using the Bray-Curtis index, as recommended for analyses of zero-inflated ecological data (Faith et al. 1987).

The significance of differences in fish communities between MPAs and fished locations within the regional seascape was investigated using PERMANOVA (Anderson 2001). The statistical design was analogous to one-way multivariate analysis of variance (MANOVA) but using permutation methods because the large number of zero records violated MANOVA assumptions associated with heterogeneity of variances. We applied unrestricted permutation of raw data and Type III sums of squares (Anderson et al. 2008).

In order to assess whether SZ sites with long-term protection differed as a group from other sites in the region, the primary planned contrast involved a PERMANOVA test of significance for 2008 data for the nine SZ sites vs. 1992–1994 data for the 10 FZ sites adjacent to MPAs plus 15 fished RZ sites in the broader region. In the case of a significant outcome, this test was followed by a contrast between 1992 data for the 9 SZ sites and 1992–1994 data for the 10 SZ and 15 RZ sites—a procedural control to assess whether SZ sites differed from other sites at the start of monitoring. Two other procedural controls, (1) contrasts of 2008 data for the 10 FZ sites vs. 1992–1994 data for the nine SZ and

[2] ⟨www.reeflifesurvey.com⟩
[3] ⟨www.fishbase.org⟩

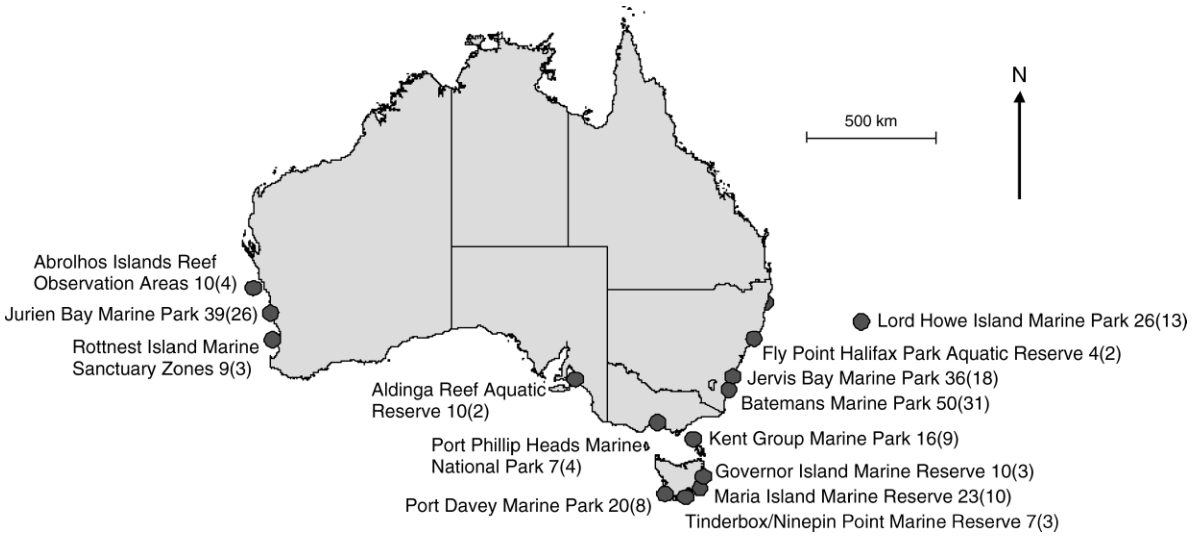

FIG. 1. Map showing investigated MPAs. The number of sites surveyed in each MPA region is shown (with number of investigated sanctuary zone sites in parentheses).

15 RZ sites and (2) 1992 data for 10 FZ sites vs. 1992–1994 data for nine SZ and 15 RZ sites, were applied to assess whether fish assemblages at reference FZ sites adjacent to the SZ sites changed over the duration of the 16-year study.

Analysis of continental patterns

Continental patterns were assessed using underwater visual census counts of fishes at 142 SZ and 125 FZ sites associated with 14 temperate and subtropical Australian MPAs. Investigated MPAs extended around ~5000 km of coast from the Abrolhos Islands (Western Australia) to Lord Howe Island (New South Wales) and around Tasmania (Fig. 1). Within each MPA, multiple transect blocks were surveyed at sites inside sanctuary zones (SZs) protected from fishing and also adjacent fished zones (FZs) that either lay outside the MPA or were designated as "general use zones" within the larger multi-zoned MPAs.

Two protocols for setting out 50-m transects at sites were used: (1) the extended transect method, as applied in the Tasmanian long-term study described above, where four 50-m transect lines were placed end-to-end along a depth contour (Edgar and Barrett 1999), and (2) the Reef Life Survey method (see footnote 2; see also Plate 1) where multiple 50-m transect lines were haphazardly distributed adjacent to the georeferenced boat mooring (Edgar and Stuart-Smith 2009). Data obtained using the two protocols are directly comparable because both are based on identical methods within each 50 × 5 m (fishes) and 50 × 1 m (invertebrates) transect block.

The extended transect method was used at 147 sites (88 SZ and 59 FZ) between June 2007 and May 2008 (mean 8 transect blocks per site). The Reef Life Survey method was applied at 120 sites (54 SZ and 66 FZ) between January and September 2008 (mean 4.6 transect blocks per site). Data from all transect blocks within a site were combined as a site mean, with site mean data then applied as replicate-level information in analyses regardless of survey method. Transect depths varied from 2.5 m to 20 m, with most transects set between 5 and 10 m depth.

MPA effects were assessed using two community metrics—the total density of fishes >45 cm length (i.e., 50-cm size class and larger) and the total biomass of fishes, with linear regression applied to quantify increase in metrics in SZs relative to FZs through time from MPA establishment. Large fish density was analyzed as a difference rather than ratio because the near absence of large fishes in FZs caused some SZ/FZ ratios to be very large and unstable. MPA age was calculated using the date of gazettal of fishing prohibitions for MPAs. The Port Phillip Heads Marine National Park included some sites protected in 1979 (within the original Harold Holt Marine Park), and others protected in 1998. The overall age of this MPA used in analyses was calculated as the mean of time of protection of SZ sites surveyed.

Because data at the continental scale were highly clumped in the vicinity of individual MPAs, site-level data possessed a high level of spatial autocorrelation, potentially greatly inflating the likelihood of Type I errors in statistical tests (Legendre 1993). As a consequence of this need to avoid spatial confounding associated with variability in the number of sites surveyed in different regions, we adopted a conservative approach to Type I errors by assigning single mean SZ and FZ values to each MPA.

RESULTS

Long-term ecological changes were highly consistent within MPAs at Maria Island and southeastern Tasma-

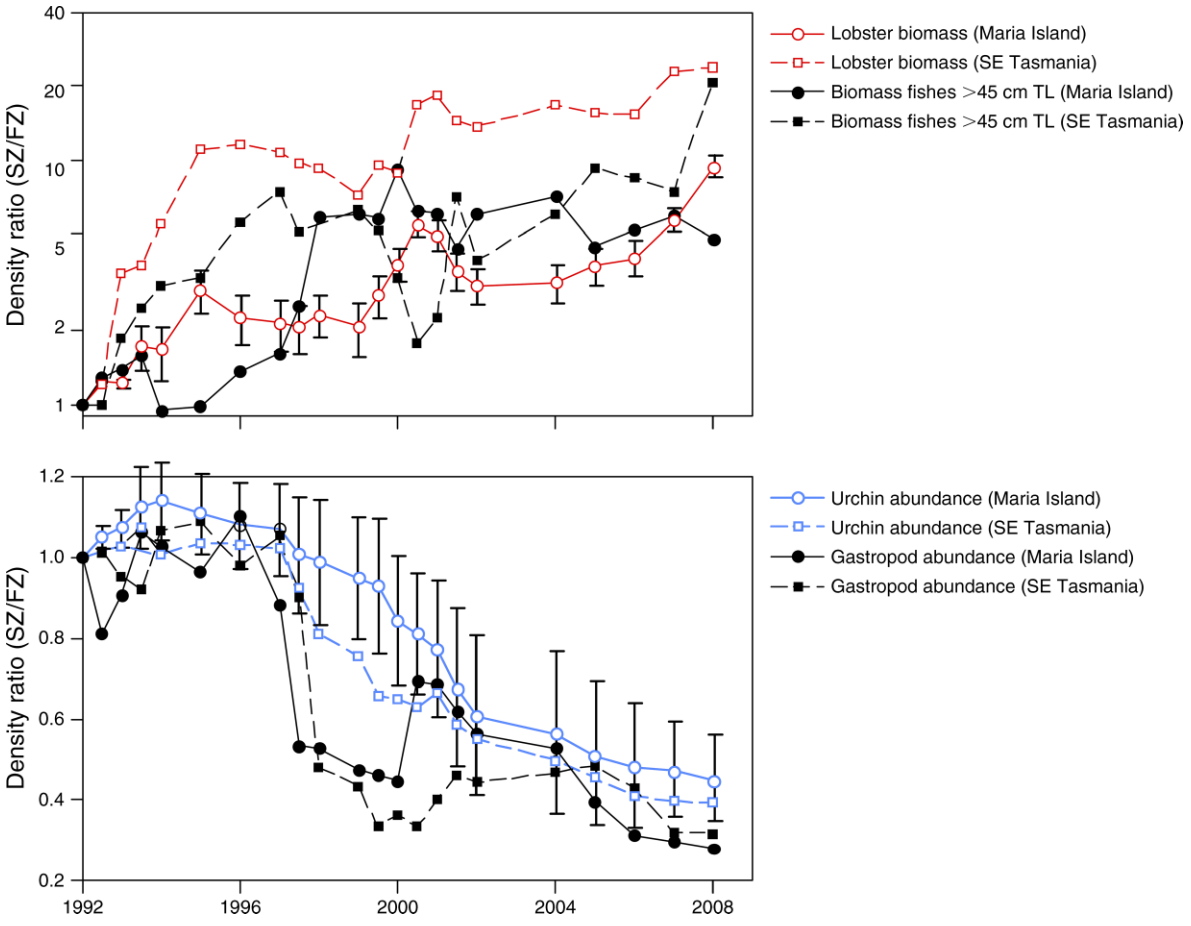

FIG. 2. Changes following MPA declaration in ratio of rock lobster biomass, large (>45 cm) fish biomass, sea urchin density, and gastropod density for sanctuary zone (SZ) sites relative to fished zone (FZ) sites in the Maria Island and southeastern Tasmanian regions. An indication of the magnitude of site variability is provided by error bars depicting the standard error of the mean for replicate sites in Maria Island SZs for lobster biomass and urchin density. Error bars were calculated using ratios that related density at each SZ site to 1992 data for the same site, rather than to FZ data as was used to calculate figured mean values.

nia, and also for two major functional groups—large predators and grazing macro-invertebrates (Fig. 2). Biomass of large fishes and rock lobsters both increased an order of magnitude over the 16-year period since MPA establishment. Lobsters sufficiently large to consume adult urchins (>120 mm carapace length; Pederson and Johnson 2006) appear to be functionally extinct outside MPAs, with only 12 animals recorded during the monitoring study in FZs compared with 312 in SZs (96.3% of total).

Densities of the two major prey groups investigated, sea urchins and gastropods, each declined ~60% in SZs within both locations. The decline followed a lag of five years (Fig. 2), a period that corresponded with the time for populations of large predators to develop within the MPAs. A total of 40 large (>120 mm carapace length) lobsters were recorded on transects within the Tasmanian MPAs in 1997, compared with an average of 3.6 large lobsters recorded in MPAs in each of the preceding five years.

After 16 years protection from fishing, fish communities at most Tasmanian SZ sites had changed markedly, lying outside the bounds of the range of communities at all studied fished sites. This is indicated by multidimensional scaling (MDS) plots showing data from 34 sites surveyed in the 1992–1994 period, and from the set of nine SZ sites and 10 FZ sites that were resurveyed using the same methods in 2008 (Fig. 3). Although a stress statistic of 0.24 indicates that the two-dimensional MDS plot is a poor summary of multidimensional pattern (Clarke 1993), presumably because of the large range of different community types included, assemblages at five of the nine SZ sites changed from within to outside the range of variation of other sites. Rotation of the three-dimensional MDS plot indicates that the third MDS axis further separates SZ from fished sites, and that seven SZ sites lie outside regional fished site variation.

A pseudo *F* test based on multivariate PERMANOVA (Anderson 2001) indicated that fish assemblages at SZ sites surveyed in 2008 were significantly different to

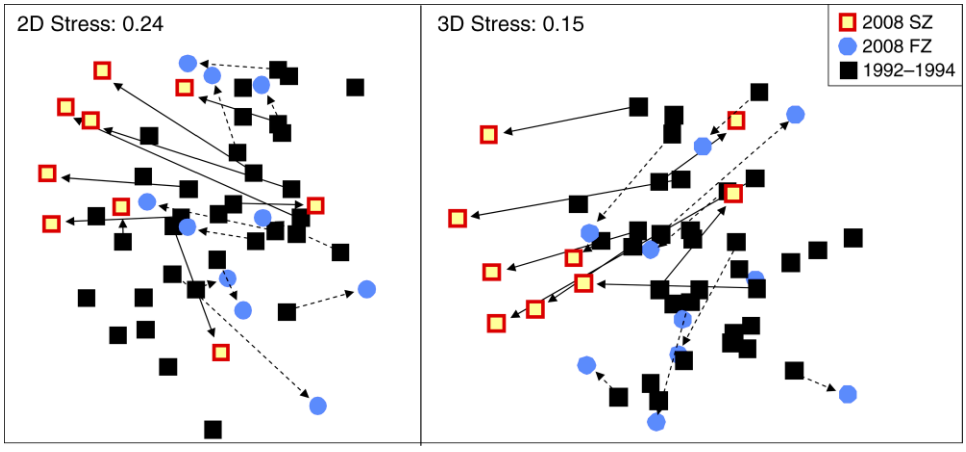

FIG. 3. Multidimensional scaling (MDS) plots relating fish biomass for different fish species at Tasmanian east coast sites. Data for 1992–1994 for all sites are plotted as solid squares, 2008 data for SZ sites as open squares, and 2008 data for FZ sites as solid circles. Arrows connect individual sites sampled in 1992 and 2008.

fished assemblages at 25 FZ+RZ sites surveyed in 1992–1994 ($F_{1,32} = 4.00$, $P = 0.0002$). This difference represented a change through time as SZ sites were not significantly different to other sites in the region at the time of MPA declaration in 1992 ($F_{1,32} = 1.09$, $P = 0.35$), nor were reference FZ sites adjacent to SZ sites different to other sites in the region in 1992–1994 ($F_{1,32} = 1.08$, $P = 0.35$) nor in 2008 ($F_{1,32} = 1.33$, $P = 0.19$).

At the level of individual sites, four SZ sites surveyed in 2008 possessed fish communities that were significantly ($P < 0.05$) different to the range in multivariate variation in sites in the 1992–1994 data set, as assessed using one-way asymmetric PERMANOVA. The four significant outcomes found in these analyses is much greater than the 0.45 Type I errors predicted for nine separate tests at $\alpha = 0.05$. None of the four SZ sites was significantly outside the range of regional site variation when surveyed in 1992–1994 (one-way PERMANOVA; $P > 0.05$).

In the continent-wide analysis, total fish biomass (B_F) and large fish density (N_{F45}) were both found to increase significantly with MPA age at SZ relative to FZ sites (T) ($\log_e(B_F) = -0.59 + 0.45 \times \log_e(T)$; $R^2 = 0.58$, $P = 0.002$; $N_{F45} = -2.02 + 1.13 \times \log(T)$; $R^2 = 0.50$, $P = 0.005$; Fig. 4). Sites in MPAs protected for 20 years averaged twice the total fish biomass present in nearby fished zones, with no indication that the trend had stabilized at 20 years.

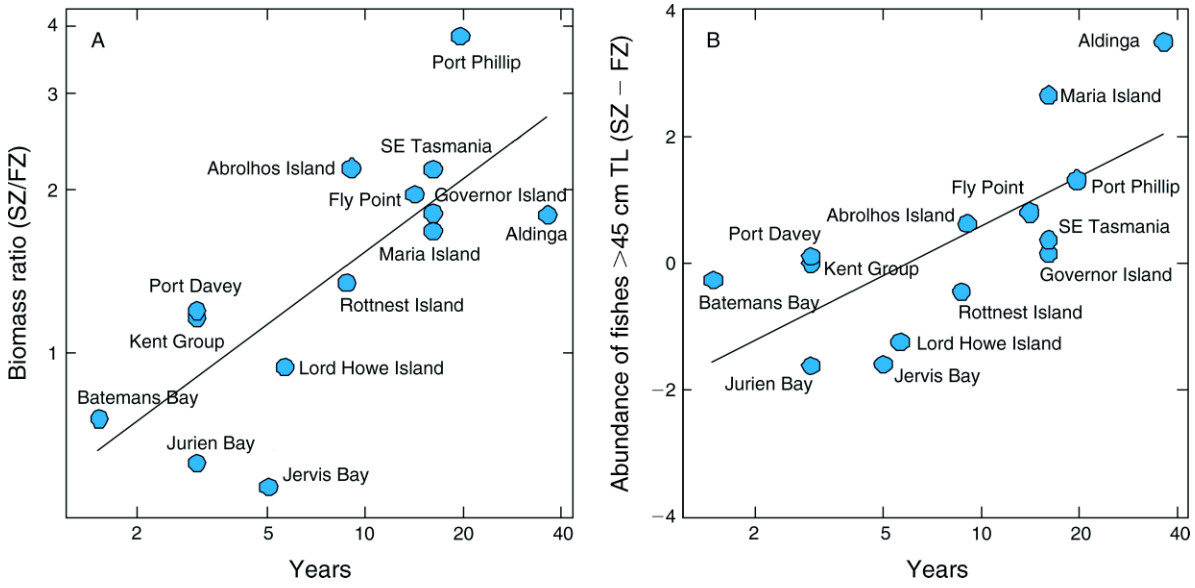

FIG. 4. Least-square regressions based on 2007–2008 continental-scale data relating period since establishment of marine protected areas (MPA) and (A) SZ/FZ ratio of fish biomass, (B) difference in density of large fishes (>45 cm total length [TL]) between SZ and FZ.

Mean fish biomass and large fish density were both lower in SZs protected for five years or less when compared with nearby FZs. At an interpolated MPA age of 1 year, regression standard errors indicated that total fish biomass was significantly lower (~60%) inside vs. outside MPAs (test SZ/FZ < 1; regression coefficient at 1 year $= -0.594$, SE $= 0.247$, $t = -2.406$, $P = 0.033$). For 1-year MPAs, density of large fishes was also significantly lower in SZs than FZs (test SZ $-$ FZ < 0; regression coefficient at 1 year $= -2.016$, SE $= 0.730$, $t = -2.760$, $P = 0.013$). Averaged across investigated MPAs, the total density of fishes >45 cm in SZs was 1.80 per 500-m^2 transect for MPAs aged six years or more, 0.35 per 500 m^2 for MPAs aged five years or less, and 0.97 per 500 m^2 in FZs. Thus, the difference in abundance relative to long-established MPAs comprises a five-fold increase if data are related to newly declared MPAs, but only a two-fold increase if data are compared to fished areas.

Discussion

Our results are consistent with the hypothesis that recently declared MPAs across Australia have been systematically located in areas with few fishery resources. Stakeholders with fishing interests presumably lobbied successfully against the "locking up" of exploitable fish stocks in SZs (Lynch 2006, Edgar et al. 2008).

If selection bias also affected the older MPAs investigated, then the effect size for the older MPAs is much larger than indicated by contemporary comparisons between sanctuary zones and adjacent fished areas (Edgar et al. 2004*b*). If, on the other hand, early MPAs had been disproportionately located in areas with high fish abundance, then patterns depicted in Fig. 4 can be explained by a change in direction of location bias over recent decades rather than ecological change within sites. This latter hypothesis is not, however, consistent with the order of magnitude of change for large fish biomass in Tasmanian MPAs after 16 years, a much greater change than evident in the continent analysis where total density of fishes >45 cm for SZs aged >6 years was about double that of FZs.

None of the Tasmanian population trends for large fishes, lobsters, sea urchins or molluscs appeared to be approaching an asymptote after 16 years. Given the continued increase in biomass of large predators, populations of grazing molluscs and echinoderms will probably decline further, with eventual flow-on effects to the next trophic level—the algal community.

Such an outcome was noted in long-term studies of the Leigh Marine Reserve in New Zealand (Shears and Babcock 2003), the only MPA worldwide where community-level data surveyed at the time the MPA was established have been compared with data obtained after >20 years. At Leigh, increased populations of lobsters and large fishes reduced sea urchin populations, which ultimately led to major changes in macroalgal cover across the MPA seascape 25 years later. Increased macroalgal cover in turn transformed the regional mosaic of habitat types, which then generated additional responses amongst other grazing invertebrate groups (Shears and Babcock 2003), a fourth order interaction (Langlois and Ballantine 2005). Changing algal cover also likely affects populations of fish and sessile invertebrate species that are closely associated with vegetated habitats (Ling 2008).

The paucity of published field studies of MPA effects undertaken over periods exceeding three years appears to have obscured general recognition of the lengthy time period required for ecosystems to respond following protection from fishing. In the two most widely cited meta-analyses of temporal MPA effects, no significant relationships were found between ecological response and time since MPA protection (Côté et al. 2001, Halpern and Warner 2002). The latter meta-analysis in fact concluded that "biological measures likely attain near-mean values within the first 1–2 years after protection" (Halpern and Warner 2002). By contrast, field studies extending more than a decade unambiguously reveal that ecological changes continue to develop in well-protected MPAs through the long term (Shears and Babcock 2003, Russ and Alcala 2004, Barrett et al. 2009).

Clearly, exclusion of human predators from heavily fished areas such as Maria Island profoundly affects marine ecosystems. By contrast, lightly fished areas have less scope for recovery after MPA declaration because fish populations have not been depleted to the same extent, while reef communities in unfished areas are unlikely to change as a direct consequence of MPA protection. Thus, while lightly fished and unfished areas possess precautionary conservation importance in MPA networks in an era of expanding resource utilization, they are unlikely to exhibit major ecological changes in response to protection.

Selective exclusion of locations with high densities of fishery resources from MPA networks may compromise biodiversity conservation goals through several mechanisms. (1) A network of lightly fished and unfished sites will generally fail to be comprehensive because it omits community types associated with heavily fished locations. Fishers arguably possess a better local knowledge of the distribution of biodiversity at the species level than can be inferred from remotely sensed habitat maps. (2) While some sites may now be lightly fished because of historic overfishing, recovery of the historic ecological communities in these locations will take considerably longer than at locations still targeted by fishers with higher densities of resource species. (3) Given the demand for fishery resources, any sites that are now lightly fished because of isolation are probably located at great distance from populated areas, hence are also likely to possess a different regional mix of species. Such sites comprise an important component of a comprehensive MPA network, but should not be regarded as representative of fished areas. (4) Protected sites that

PLATE 1. Volunteer diver undertaking fish transect in the Abrolhos Islands, Australia. Photo credit: G. J. Edgar.

were formerly heavily fished are needed as scientific reference areas for improved understanding and management of effects of fishing, including disentangling fishing impacts from factors such as climate change. Without reference sites that are unfished but are otherwise comparable to fished sites, the contribution of fishing to long term regional change cannot be rigorously distinguished.

Over the long term, declaration of MPAs at fished sites adds additional communities to the regional mosaic, increasing biodiversity at the seascape level through elevated abundances of species targeted by fishers plus those positively affected by third-order trophic interactions. By contrast, other species will predictably decrease in abundance in MPA patches through negative secondary and fourth-order trophic interactions. Heavily fished communities should be regarded as priority targets in MPA conservation networks because they will undergo greatest ecological recovery and transformation following cessation of fishing, thereby contributing most to expansion in regional heterogeneity of biodiversity.

Highly fished areas should additionally be recognized as priority targets within MPA networks because a high level of human-induced disturbance generates high site vulnerability and a relatively high proportion of species at risk of extinction (Pressey 1994, Edgar et al. 2008). If subsets of such habitats and associated species are not protected now then with further disturbance the habitat and species could be completely lost (Langhammer et al. 2007).

This is not to argue that MPA networks should predominantly comprise heavily fished locations. Clearly, when equivalent community types are available for reservation, one with high existing resource usage and another without, then the unexploited community represents a higher priority target for protection. In many situations, the unexploited community may also represent the only socially acceptable option for protection. Regardless, without safeguarding at least some locations that were formerly heavily fished, the MPA network will fail comprehensiveness, adequacy and representativeness criteria. Marine conservation planners could usefully learn from their terrestrial counterparts, who generally now recognize that ad hoc networks of protected areas based on locations with little resource value (e.g., mountain tops and arid lands)—"the lands nobody wanted" (Shands and Healey 1977)—are biased and can ultimately make the goal of safeguarding the full range of regional biodiversity more expensive (Pressey 1994, Margules and Pressey 2000).

In summary, fishing generates a series of trophic cascades in temperate reef ecosystems (Tegner and Dayton 1999, Clemente et al. 2009)—population densities of large predators catastrophically decline, densities of grazing invertebrates increase, and algal communities change, with additional ripples through the food web as habitats transform. Once fishing ceases, each of these trophic steps adds time lags of many years before the ecosystem can be considered fully recovered. Given the global ubiquity of fishing impacts (Jackson et al. 2001), and the fact that no long-term MPA monitoring study to date has apparently surpassed the time required for complete ecological recovery (Willis et al. 2003), the full effects of fishing on coastal reefs are best regarded as still unknown.

Acknowledgments

We thank Peter Bosworth, Alex Schaap, Howell Williams, and Colin Buxton for facilitating the Tasmanian MPA monitoring program, and numerous colleagues and assisting divers, particularly Kevin Bancroft, Bill Barker, James Brook, Jon Bryan, Antonia Cooper, Kevin Crane, Marlene Davey, Tom Davis, Paul Day, Sam Ibbott, Andrew Green, Rebecca Koss, Don Love, Tim Lynch, Bryan McDonald, Alistair Morton, Sue Newson, Ariana Polacheck, Ian Shaw, Scoresby Shepherd, Kevin Smith, Margo Smith, Ashley Smith, and Simon Wilcox. The project was supported by the Commonwealth Environment Research Facilities program and Australian Research Council.

Literature Cited

Anderson, M. J. 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecology 26:32–46.

Anderson, M. J., R. N. Gorley, and K. R. Clarke. 2008. PERMANOVA+ for PRIMER: guide to software and statistical methods. PRIMER-E, Plymouth, UK.

Barrett, N. S., C. D. Buxton, and G. J. Edgar. 2009. Changes in invertebrate and macroalgal populations in Tasmanian marine reserves in the decade following protection. Journal of Experimental Marine Biology and Ecology 370:104–119.

Clarke, K. R. 1993. Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology 18:117–143.

Clemente, S., J. C. Hernández, and A. Brito. 2009. Evidence of the top-down role of predators in structuring sublittoral rocky-reef communities in a Marine Protected Area and nearby areas of the Canary Islands. ICES Journal of Marine Science 66:64–71.

Côté, I. M., I. Mosqueira, and J. D. Reynolds. 2001. Effects of marine reserve characteristics on the protection of fish populations: a meta-analysis. Journal of Fish Biology 59(Supplement A):178–189.

Edgar, G. J., and N. S. Barrett. 1999. Effects of the declaration of marine reserves on Tasmanian reef fishes, invertebrates and plants. Journal of Experimental Marine Biology and Ecology 242:107–144.

Edgar, G. J., N. S. Barrett, and A. J. Morton. 2004*a*. Biases associated with the use of underwater visual census techniques to quantify the density and size-structure of fish populations. Journal of Experimental Marine Biology and Ecology 308:269–290.

Edgar, G. J., R. H. Bustamante, J.-M. Fariña, M. Calvopiña, C. Martinez, and M. V. Toral-Granda. 2004*b*. Bias in evaluating the effects of marine protected areas: the importance of baseline data for the Galapagos Marine Reserve. Environmental Conservation 31:212–218.

Edgar, G. J., et al. 2008. Key Biodiversity Areas as globally significant target sites for the conservation of marine biological diversity. Aquatic Conservation: Marine and Freshwater Ecosystems 18:969–983.

Edgar, G. J., J. Moverley, N. S. Barrett, D. Peters, and C. Reed. 1997. The conservation-related benefits of a systematic marine biological sampling program: the Tasmanian reef bioregionalisation as a case study. Biological Conservation 79:227–240.

Edgar, G. J., and R. D. Stuart-Smith. 2009. Ecological effects of marine protected areas on rocky reef communities: a continental-scale analysis. Marine Ecology Progress Series, *in press*.

Faith, D. P., P. R. Minchin, and L. Belbin. 1987. Compositional dissimilarity as a robust measure of ecological distance. Vegetatio 69:57–68.

Halpern, B. S., and R. R. Warner. 2002. Marine reserves have rapid and lasting effects. Ecology Letters 5:361–366.

Harborne, A. R., P. J. Mumby, C. V. Kappel, C. P. Dahlgren, F. Micheli, K. E. Holmes, and D. R. Brumbaugh. 2008. Tropical coastal habitats as surrogates of fish community structure, grazing and fisheries value. Ecological Applications 18:1689–1701.

Jackson, J. B. C., et al. 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science 293:629–638.

Klein, C. J., A. Chan, L. Kircher, A. J. Cundiff, N. Gardner, Y. Hrovat, A. Scholz, B. E. Kendall, and S. Airame. 2008. Striking a balance between biodiversity conservation and socioeconomic viability in the design of marine protected areas. Conservation Biology 22:691–700.

Langhammer, P. F., et al. 2007. Identification and gap analysis of Key Biodiversity Areas: targets for comprehensive protected area systems. IUCN Best Practice Protected Areas Guidelines Series No. 15. IUCN, Gland, Switzerland.

Langlois, T. J., and W. Ballantine. 2005. Marine ecological research in New Zealand: developing predictive models through the study of no-take marine reserves. Conservation Biology 19:1763–1770.

Legendre, P. 1993. Spatial autocorrelation: trouble or new paradigm? Ecology 74:1659–1673.

Leslie, H. M. 2005. A synthesis of marine conservation planning approaches. Conservation Biology 19:1701–1713.

Ling, S. D. 2008. Range expansion of a habitat-modifying species leads to loss of taxonomic diversity: a new and impoverished reef state. Oecologia 156:883–894.

Lynch, T. P. 2006. Incorporation of recreational fishing effort into design of marine protected areas. Conservation Biology 20:1466–1476.

Margules, C. R., and R. L. Pressey. 2000. Systematic conservation planning. Nature 405:243–253.

Pederson, H. G., and C. R. Johnson. 2006. Predation of the sea urchin *Heliocidaris erythrogramma* by rock lobsters (*Jasus edwardsii*) in no-take marine reserves. Journal of Experimental Marine Biology and Ecology 336:120–134.

Pressey, R. L. 1994. Ad hoc reservations: forward or backward steps in developing representative reserve systems? Conservation Biology 8:662–668.

Richardson, E. A., M. J. Kaiser, G. Edwards-Jones, and H. P. Possingham. 2006. Sensitivity of marine-reserve design to the spatial resolution of socioeconomic data. Conservation Biology 20:1191–1202.

Russ, G. R., and A. C. Alcala. 2004. Marine reserves: long-term protection is required for full recovery of predatory fish populations. Oecologia 138:622–627.

Shands, W. E., and R. G. Healey. 1977. The lands nobody wanted. Conservation Foundation, Washington, D.C., USA.

Shears, N. T., and R. C. Babcock. 2003. Continuing trophic cascade effects after 25 years of no-take marine reserve protection. Marine Ecology Progress Series 246:1–16.

Smith, R. J., P. D. Eastwood, Y. Ota, and S. I. Rogers. 2009. Developing best practice for using Marxan to locate marine protected areas in European waters. ICES Journal of Marine Science 66:188–194.

Tegner, M. J., and P. K. Dayton. 1999. Ecosystem effects of fishing. Trends in Ecology and Evolution 14:261–262.

United Nations Environment Programme. 2005. COP decision VII/5: marine and coastal biological diversity. ⟨http://www.cbd.int/decision/cop/?id=7742⟩

Walters, C. J., and C. S. Holling. 1990. Large-scale management experiments and learning by doing. Ecology 71:2060–2068.

Williams, A., N. J. Bax, R. J. Kloser, F. Althaus, B. Barker, and G. Keith. 2009. Australia's deep-water reserve network: implications of false homogeneity for classifying abiotic surrogates of biodiversity. ICES Journal of Marine Science 66:214–224.

Willis, T. J., R. B. Millar, R. C. Babcock, and N. Tolimieri. 2003. Burdens of evidence and the benefits of marine reserves: putting Descartes before des horse? Environmental Conservation 30:97–103.